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NEW SERIES, NO. 27

**Status of the Pachypleurosauroid
Psilotrachelosaurus toeplitschi
Nopcsa (Reptilia, Sauropterygia), from
the Middle Triassic of Austria**

Olivier Rieppel

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**Status of the Pachypleurosauroid
Psilotrachelosaurus toeplitschi
Nopcsa (Reptilia, Sauropterygia), from
the Middle Triassic of Austria**

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Table of Contents

ABSTRACT 1

INTRODUCTION 1

MATERIAL 2

THE GEOLOGICAL PROVENANCE OF
 PSILOTRACHELOSAURUS TOEPLITZSCHII 2

SYSTEMATIC PALEONTOLOGY 4

DISCUSSION 10

CONCLUSIONS 15

ACKNOWLEDGMENTS 15

LITERATURE CITED 15

List of Tables

1. Measurements of metatarsal and phalan-
geal length in the right pes of *Psilotrache-*
losaurus toeplitzschii 9

2. Number of dorsal vertebrae and limb
proportions in *Psilotrachelosaurus toeplit-*
zschii, compared to *Serpianosaurus* and
Neusticosaurus 12

3. Data matrix for cladistic analysis of pachy-
pleurosauroid interrelationships 13

List of Illustrations

1. Map of the Kellerberg-Quarry and the
Stadelbachgraben in the Gailtaler Alps ... 3

2. Holotype of *Psilotrachelosaurus toeplit-*
zschii 5

3. Pectoral girdle of *Psilotrachelosaurus toep-*
litzschii 6

4. Pelvic girdle of *Psilotrachelosaurus toeplit-*
zschii 7

5. Pubis in pachypleurosauroids 8

6. Appendicular skeleton of *Psilotrachelo-*
saurus toeplitzschii 8

7. Right humerus of *Psilotrachelosaurus toep-*
litzschii 9

8. Humeri of *Dactylosaurus schroederi* 11

9. Cladogram of pachypleurosauroid inter-
relationships 14

Status of the *Pachypleurosauroid* *Psilotrachelosaurus toeplitschi* Nopcsa (Reptilia, Sauropterygia), from the Middle Triassic of Austria

Olivier Rieppel

Abstract

The redescription of the holotype and only known specimen of *Psilotrachelosaurus toeplitschi* Nopcsa, 1928, from the northern Alps of Austria, and its comparison with other pachypleurosauroids show the specimen to represent a distinct genus and species. It is the sister-taxon of the *Serpianosaurus*–*Neusticosaurus* clade from the Middle Triassic of Central and Southern Europe (German Lettenkeuper as well as Grenzbitumenzone and Meridekalke of the southern Alps in southern Switzerland and Italy). *Psilotrachelosaurus* is represented by a subadult (sex y) or a small but already sexually mature (sex x) individual. Diagnostic features of the specimen include body proportions (relatively short humerus as compared to standard length), ossified distal carpal and tarsal 4, and a relatively broad pubis.

Introduction

In 1928, Nopcsa described a specimen of a small sauropterygian as a new genus and species, *Psilotrachelosaurus toeplitschi*. The exact locality and stratigraphical horizon of the fossil remain unknown, but the dark (blackish) and bituminous limestone surrounding the fossil led Nopcsa (1928) to conclude that it came from the Alpine Muschelkalk series (Triassic) as it crops out in the Stadelbachgraben, 2 km west of Töplitsch in the northern Alps of Austria (Huene, 1956, p. 84, suggested a Ladinian age; see the discussion below).

Nopcsa (1928) classified the new genus within his family Nothosauridae, along with *Phygosaurus* (a nomen dubium; Rieppel, 1989a), *Lariosaurus*, *Macromerosaurus* (a junior synonym of *Lariosaurus*; see Rieppel, 1987, for a discussion), *Rhaeticonia* (a problematical taxon of which the type and only known specimen is lost; Rieppel, 1987), *Nothosaurus*, *Germanosaurus* (another taxon of questionable validity, perhaps *Cymatosaurus*; Storrs, 1991), *Cymatosaurus*, and *Pistosaurus*. Following the discovery of abundant pachypleurosaur material in the Grenzbitumenzone (Anisian–Ladinian boundary) of Monte San Giorgio (southern Alps of Switzerland) and the redescription

of the *Lariosaurus* and *Pachypleurosaurus* (a junior synonym of *Neusticosaurus*; see Sander, 1989, for a discussion) material from Perledo (upper Ladinian or lower Carnian, southern Alps of northern Italy), Peyer (1934) concluded (without inspection of the original) that *Psilotrachelosaurus* in fact belongs to the family Pachypleurosauridae (along with *Anarosaurus*, *Dactylosaurus*, *Neusticosaurus*, “*Pachypleurosaurus*,” and “*Phygosaurus*”). This conclusion was accepted by Zangerl (1935) in his description of “*Pachypleurosaurus edwardsii*” from Monte San Giorgio, who added that he had, in fact, been unable to detect characters that separate *Psilotrachelosaurus* from “*Pachypleurosaurus*” at the generic level (again without inspection of the original). Zangerl (1935, p. 69) denied that any major taxonomic importance could be attached to limb proportions or to the number of presacral vertebrae in this group. He questioned Nopcsa’s (1928) description of the diagnostic coracoid of *Psilotrachelosaurus* and found Nopcsa’s claim that all five metatarsals are of equal length to be refuted by Nopcsa’s figure of the specimen (1928, pl. II fig. 1). Huene (1956) retained the genus as distinct from “*Pachypleurosaurus*,” but Kuhn-Schnyder (1959, p. 654) once more questioned its validity, noting similarities in the

structure of the carpus that *Psilotrachelosaurus* shares with "*Pachypleurosaurus*." He also indicated that the Monte San Giorgio material required revisionary work (Kuhn-Schnyder, 1959, p. 655), since more than the one species (e.g., *P. edwardsii*) described by Zangerl (1935) appeared to be present. Sues and Carroll (1985) once again doubted Nopcsa's (1928) description of the coracoid and concluded that "[t]oo little is known about . . . *Psilotrachelosaurus* at present to allow a definitive phylogenetic assessment" (Sues & Carroll, 1985, p. 1608). It was obvious that the proper assessment of the affinities of *Psilotrachelosaurus* had to be based on a revision of the abundant Monte San Giorgio material (Zapfe & König, 1980, p. 78), a task that has now been completed (Carroll & Gaskill, 1985; Rieppel, 1989a; Sander, 1989). It is on the basis of this background that the type specimen of *Psilotrachelosaurus toeplitzschii* is here redescribed.

Material

The holotype and only known specimen of *Psilotrachelosaurus toeplitzschii* Nopcsa is housed at the Landesmuseum für Kärnten (Dept. of Mineralogy and Geology, collection Nr. 201) in Klagenfurt, Austria. The specimen is embedded in a dark bituminous limestone. The original handwritten label attached to the specimen reads "*Stadelbachgraben (?) bei Töplitzsch*."

A cast of *Anarosaurus pumilio*, kept at the Staatliches Museum für Naturkunde in Stuttgart, Germany, was used for comparison, as well as material of *Dactylosaurus* cf. *D. schroederi* kept at the Museum für Historische Geologie und Paläontologie, University of Tübingen, Germany (GPTI 1744/1-10; see fig. 8).

The Geological Provenance of *Psilotrachelosaurus toeplitzschii*

The geological provenance of *Psilotrachelosaurus* is difficult to reconstruct and requires some discussion. The holotype and only known specimen was collected in 1844, and lithological clues indicate the Stadelbachgraben, 2 km west of Töplitzsch (Kärnten) in the Gailtaler Alps, northern Alps of Austria (Tollmann, 1977), as the likely locality (fig. 1). The geological map of Austria (An-

derle, 1977) shows the Stadelbachgraben to cut through a succession of Triassic deposits, ranging from the lower Anisian up to the Carnian (for more details on the geology of the Gailtaler Alps, see Bechstädt & Mostler, 1974; Bechstädt et al., 1976; Hauser, 1982).

All indications are that *Psilotrachelosaurus* comes from the Partnach-Plattenkalk (Warch, 1979; also known as Partnachschichten or "Plattenkalk" [Zapfe & König, 1980]), which for its greater part is Ladinian but has been claimed to extend down into the latest Anisian (Tollmann, 1977, p. 605). Apart from *Psilotrachelosaurus*, the Middle Triassic of the Gailtaler Alps has produced two other, poorly preserved pachypleurosaurs, but also two specimens (one of which is rather well preserved although incomplete) of *Lariosaurus* cf. *L. balsami* (Warch, 1966, 1979; Zapfe & König, 1980). Both specimens of *Lariosaurus* were found in the Kellerberg-Quarry, located immediately east of the Stadelbachgraben and between the towns of Stadelbach and Kellerberg. Since outcrops in the Stadelbachgraben can be correlated to the sequence of layers exposed in the Kellerberg-Quarry, the stratigraphical relations of the *Lariosaurus* specimens from the Kellerberg-Quarry may point to equivalent layers in the Stadelbachgraben that have produced the *Psilotrachelosaurus* specimen.

The Partnach-Plattenkalk lies on top of the Zwischendolomit of late Anisian age (the Zwischendolomit is the uppermost of three units of the Alpine Muschelkalk series [Warch, 1979; cf. Nopcsa, 1928]). A stratigraphic analysis of the Partnach-Plattenkalk in the Kellerberg-Quarry has identified three units: a lower unit of limestone, an intercalated bed of "marly shales" at the middle of the lithostratigraphical column of the Partnach-Plattenkalk (Warch, 1979, p. 36, 1984), and an upper unit of limestone. Originally believed to represent the early Ladinian only (Warch, 1979), the Partnach-Plattenkalk is now thought to represent the entire suite of Ladinian deposits in the Gailtaler Alps (Bechstädt et al., 1976; Warch, 1984, and in lit. 10 Nov. 1992).

According to Zapfe & König (1980), the greater part of the Kellerberg-Quarry is located in the upper unit of the Partnach-Plattenkalk, which to them represents the late Ladinian. This led these authors to conclude that the *Lariosaurus* specimens mentioned by Warch (1966, 1979) come from the late Ladinian, and the same is postulated for *Psilotrachelosaurus*. Zapfe and König (1980) supported their conclusions with a comparison of the upper part of the Partnach-Plattenkalk to the Cal-



FIG. 1. A map showing the location of the Kellerberg-Quarry and the Stadelbachgraben in the Gailtaler Alps.

care di Perledo of the southern Alps (northern Italy), also claimed to be of late Ladinian age, perhaps extending into the Carnian (Tintori et al., 1985; Gaetani et al., 1992). A comparison of the upper unit of the Partnach-Plattenkalk with the Calcare di Perledo (Zapfe & König, 1980) had been proposed earlier on the basis of the occurrence of an actinopterygian fish, *Ophiopsis lariensis*, at both localities (Sieber, 1955; see also Tollmann, 1977, p. 585). The comparison of the Partnach-Plattenkalk to the Calcare di Perledo is interesting, since these are the only two localities known so far where lariosaurs and pachypleurosaurs occur together (but

see the discussion below). However, the stratigraphical relations of the vertebrate fossils from the Calcare di Perledo remain uncertain, and *Ophiopsis* has also been found in the Prosanto Formation of the Swiss Alps, believed to be of early to middle Ladinian age (Bürgin et al., 1991). *Ophiopsis* remains unknown from Monte San Giorgio (Grenzbitumenzone, Anisian–Ladinian boundary).

The possibility that *Psilotrachelosaurus* comes from a horizon at the transition from the Zwischendolomit to the Partnach-Plattenkalk (Anisian–Ladinian boundary) can be ruled out, because

nowhere in the Kellerberg-Quarry nor in the Stadelbachgraben are the corresponding layers exposed (Warch, in lit. 10 Nov. 1992, contra Zapfe & König, 1980; this transition is likewise not indicated in the Kellerberg profile published by Zapfe & König, 1980, fig. 2). Furthermore, the *Lariosaurus* specimens from the Kellerberg-Quarry were found immediately above the intercalated bed of marly shales within the Partnach-Plattenkalk, which indicates a middle Ladinian age (Warch, 1984). Identical lithological and stratigraphical relations in the Stadelbachgraben indicate an equivalent age for *Psilotrachelosaurus* (Warch, in lit. 10 Nov. 1992).

Systematic Paleontology

Sauropterygia Owen, 1860

Pachypleurosauroidea Huene, 1956

Pachypleurosauridae Nopcsa, 1928

***Psilotrachelosaurus* Nopcsa, 1928**

TYPE SPECIES—*Psilotrachelosaurus toeplitzschii* Nopcsa, 1928.

GENERIC DIAGNOSIS—A small-sized pachypleurosaur sharing with the *Serpianosaurus*–*Neusticosaurus* clade the surface ornamentation on the humerus but differing by the relatively short humerus, a more fully ossified carpus and tarsus (distal carpal/tarsal 4 present), and relatively broad ventral elements in the pelvic girdle.

DISTRIBUTION—Middle Triassic (middle Ladinian), the Stadelbachgraben, Gailtaler Alps, Austria.

***Psilotrachelosaurus toeplitzschii* Nopcsa, 1928**

HOLOTYPE—Landesmuseum für Kärnten, Dept. of Mineralogy and Geology, Nr. 201.

DIAGNOSIS—Same as for genus, of which this is the only known species.

DISTRIBUTION—Same as for genus, of which this is the only known species.

MORPHOLOGICAL DESCRIPTION—The total length of the specimen as preserved (fig. 2) is 115.8 mm. It comprises most of the cervical vertebral column, the entire trunk region and appendicular skeleton, and proximal parts of the tail. The specimen is exposed in ventral view. The distance between glenoid and acetabulum is 56 mm; the standard length (Rieppel, 1989a; Sander, 1989), defined as

the length of the last four presacral (dorsal) vertebrae, is 12 mm.

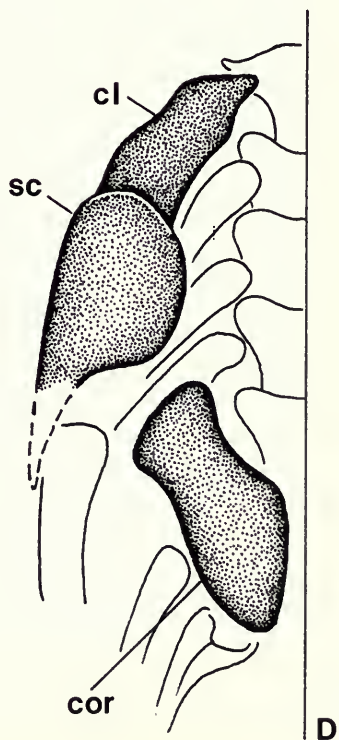
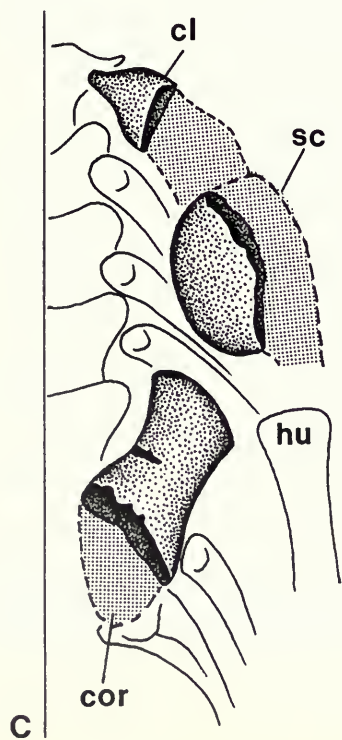
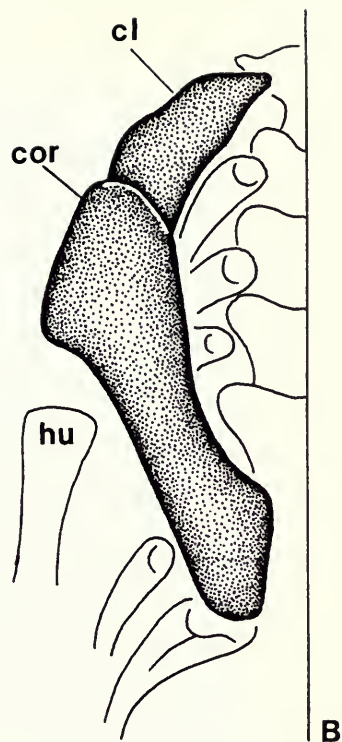
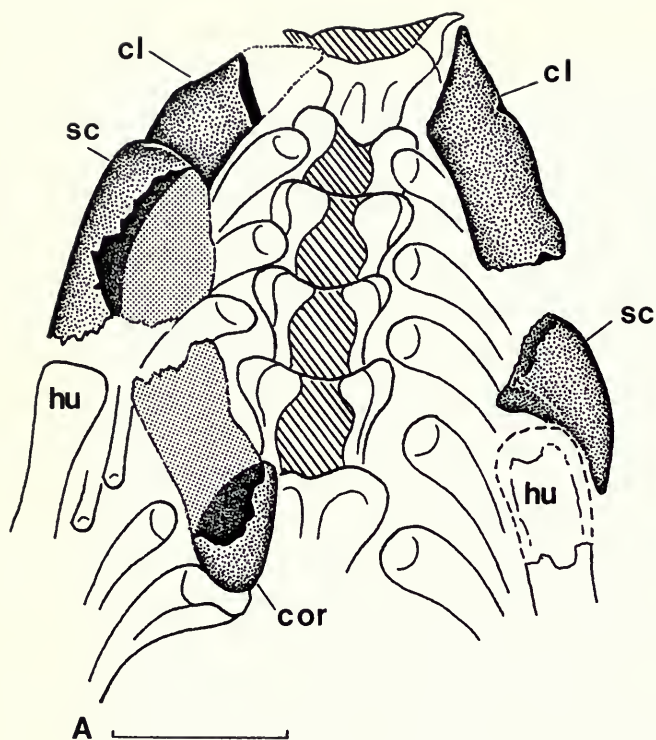
A total of 12 cervical vertebrae (the anterior-most one incompletely preserved) can be counted (see also Nopcsa, 1928). The neural arch has separated from the centrum at the neurocentral suture in the last four cervicals (in front of the pectoral girdle), such that the fossil displays the ventral (internal) view of the well-defined neural canal. The remaining eight cervical vertebrae are preserved only as natural molds. Nopcsa (1928) considered the last four cervical vertebrae to be distinctly elongated (longer than broad). However, actual measurements across the length and total width of the neural arch (as preserved, in ventral view) do not corroborate this impression: the penultimate (and best preserved) neural arch is 2.7 mm long and at least 2.8 mm wide (maximally 3.1 mm). Comparison of the mold and the cast of the specimen indicates a relative increase in length of the cervical vertebrae from front to back. Cervical ribs cannot be identified on the fossil due to poor preservation.

A total of 19 dorsal vertebrae can be counted. In most of them the centrum has again separated from the neural arch at the neurocentral suture, leaving the neural arch exposed in ventral view. The lower surface of the centrum is at least partially preserved in the first and last dorsal vertebra. As described by Nopcsa (1928), the ventral surface of the anterior dorsal vertebra shows two slight ridges converging anteriorly. The ventral surface of the centrum of the posterior dorsal vertebra shows a vermiculate ornamentation. The dorsal ribs show very pronounced pachyostosis in their proximal part.

The structure of the sacral region is obscured by the elements of the pelvic girdle, but three sacral ribs can unequivocally be identified (see below and fig. 4). The first sacral rib as well as the first sacral vertebra is exposed through the thyroid foramen between pubis and ilium. On either side, the pubis shows a well-defined obturator foramen at its posterior margin close to the acetabulum (see below), through which the underlying matrix is clearly identifiable. This indicates that no anterior sacral rib is covered by the pubes. Oblique light reveals two additional sacral ribs covered by the right ischium as exposed on the left side of the fossil, bringing the total number of sacral ribs up to three. On the left side of the fossil (exposed on the right side), the relation of the posterior margin of the ischium and of the third sacral rib is obscured. The second and third sacral vertebrae are partially



FIG. 2. Holotype and only known specimen of *Psilotrachelosaurus toeplitschi* Nopcsa. Approximately 1.5 times natural size.



exposed (in ventral view) between the symphyseal edges of the ischium of either side. The sacral ribs appear to be straight and relatively robust elements, pachyostotic throughout, but without significant distal expansion. Morphological details are obscured by the overlying ischia.

A small number of at least six proximal caudal vertebrae are preserved, but preparation has destroyed all morphological detail. However, at least two pairs of caudal ribs can be clearly identified. The first caudal rib is associated with the first caudal vertebra, and the caudal ribs are not fused to their respective vertebrae (fig. 2).

Delicate impressions between the proximal parts of the dorsal ribs, particularly in the middle and anterior part of the right body side, indicate the presence of gastral ribs. No information is available on the detailed structure of the "ventral ribs," such as the number of segments in each rib.

As described by Nopcsa (1928), the pectoral girdle of *Psilotrachelosaurus* (figs. 3A–D) has raised questions in regard to the apparently peculiar shape of the coracoid (Zangerl, 1935; Sues & Carroll, 1985). The interclavicle is not preserved. The clavicle is preserved on both sides, showing the impression of its tapering anterior end on the right side (more obvious in the latex mold of the fossil). The left clavicle appears to end posteriorly in a broad transverse margin, but this may be the result of breakage. Behind it, the narrow and tapering dorsal wing of the left scapula is partially exposed at the proximal end of the left humerus. On the right side, the clavicle disappears below the broken anterior end of a bone, which Nopcsa (1928) interpreted as the coracoid (fig. 3A). Close to the vertebral column, the broken medial head of the right coracoid can be identified. Between the latter two bone fragments, a shallow area indicates the natural mold of a bone surface; the natural bone has been torn off and lost as part and counterpart of the fossil separated (fig. 3A). According to Nopcsa (1928, p. 34), "Of the coracoids only the proximal and distal end of the right coracoid has been preserved. The middle part of the right coracoid broke away, but left a neat impression. To bring this part of the shoulder-girdle out more clearly, later on this impression has carefully been filled up with plaster and afterwards painted black.

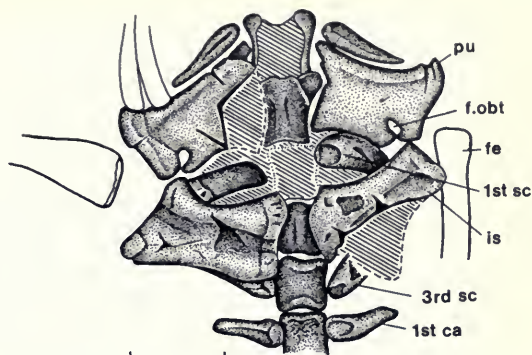


FIG. 4. The pelvic girdle of *Psilotrachelosaurus toeplitzschii* Nopcsa as preserved in ventral view. Scale bar equals 5 mm. Abbreviations: fe, femur; f. obt, obturator foramen; is, ischium; pu, pubis; 1st ca, first caudal rib; 1st sc, first sacral rib; 3rd sc, third sacral rib.

Thus the general outline of the bone is well shown . . . " (fig. 3B). This plaster filling has now been removed, with no indication as to when and how this happened. Removal of the plaster shows that the supposed coracoid was broken across the broad (pachyostotic) proximal portion of a dorsal rib, separating the two fragments to a degree that would add to the impression of an unduly elongated coracoid. Careful investigation of a latex peel of the specimen furthermore indicates that this dorsal rib separated a distal bone, the right scapula, from a proximal (medial) bone, the right coracoid (fig. 3C). Combining the drawings obtained from the type specimen and from the latex peel reveals a fragmentary preservation of the right scapula, at the proximal head of the right humerus, and a right coracoid of typical pachypleurosauroid proportions (fig. 3D).

In the pelvic girdle (fig. 4), the ilium is not exposed on either side. The shape and relations of the pubis and ischium are difficult to determine because of the underlying sacral ribs. The right pubis shows a broad acetabular portion, ventral (medial) to which the obturator foramen can be identified as a slit-like opening in the posterior margin of the bone. The posterior opening of the obturator foramen is narrow, but not entirely closed as it is in the left pubis (where a "suture" remains visible). The ventral part of the right pubis is bro-

FIG. 3. The pectoral girdle of *Psilotrachelosaurus toeplitzschii* Nopcsa. A, the specimen as preserved in ventral view; B, Nopcsa's (1928) interpretation of the morphology of the right coracoid bone; C, drawing of the latex mold of the right side of the pectoral girdle; D, reconstruction of the right side of the pectoral girdle in ventral view. Scale bar equals 5 mm. Abbreviations: cl, clavicle; cor, coracoid; hu, humerus; sc, scapula.

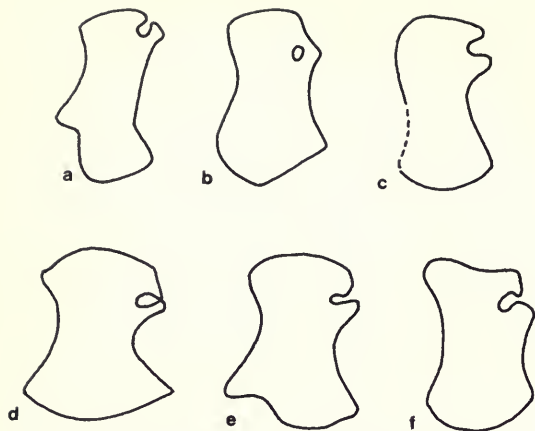


FIG. 5. Outlines and proportions of the pubis in pachypleurosauroids. a, *Anarosaurus pumilio* (original, after a cast at the Staatliches Museum für Naturkunde, Stuttgart); b, *Dactylosaurus schroederi* (after Sues and Carroll, 1985); c, *Neusticosaurus peyeri* (after Sander, 1989); d, *Neusticosaurus edwardsii* (after Carroll and Gaskill, 1985); e, *Serpianosaurus mirigiolensis* (after Rieppel, 1989a); f, *Psilotrachelosaurus toeplitzschii* (original).

ken, but the left pubis indicates concave posterior and anterior margins that define a bone of greater relative width than is usually observed in pachypleurosaurs (Huene, 1956, p. 384), which show a more distinctly "waisted" appearance of the bone (fig. 5).

The shape of the ischium is even harder to determine since the bone is broken across two sacral ribs. The anterior margin of the ischium is concave and, together with the concave posterior margin of the pubis, indicates the presence of a thyroid foramen. The posterior margin of the ischium cannot be unequivocally determined on the right side, and on the left side it is obscured by breakage caused by the sacral ribs. The posterior margin appears to lie at the level of the third sacral rib, which would again indicate a greater width of the ischium than is usually observed among pachypleurosaurs.

The right forelimb is better preserved than the left (figs. 6A,B). The humerus is typically pachypleurosauroid (Peyer, 1934), with a slight curvature, a weakly developed deltopectoral crest, and a slight distal expansion. The entepicondyle is not pronounced, but the entepicondylar foramen is well defined, fully enclosed by bone, and separated by about 0.5 mm from the distal articular surface of the humerus. The bone surface shows a distinct ornamentation (fig. 7) of grooves and ridges on the expanded proximal and distal heads. The groove

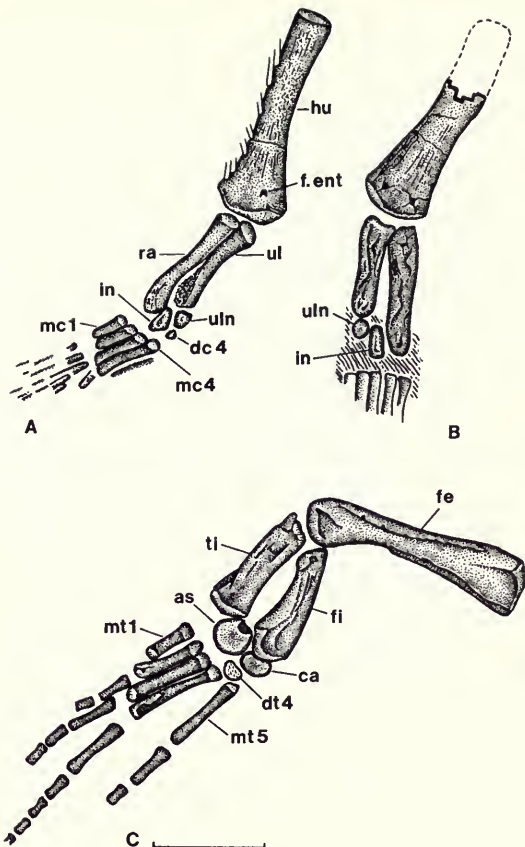


FIG. 6. The appendicular skeleton of *Psilotrachelosaurus toeplitzschii* Nopcsa, as preserved in ventral view. A, right forelimb; B, left forelimb; C, right hindlimb. Scale bar equals 5 mm. Abbreviations: as, astragalus; ca, calcaneum; dc4, distal carpal 4; dt4, distal tarsal 4; fe, femur; f. ent, entepicondylar foramen; fi, fibula; hu, humerus; in, intermedium; mc1, metacarpal 1; mc4, metacarpal 4; mt1, metatarsal 1; mt4, metatarsal 4; mt5, metatarsal 5; ra, radius; ti, tibia; ul, ulna; uln, ulnare.

and ridge pattern becomes more closely spaced, anastomoses become more frequent, and the surface ornamentation assumes a more vermiculate appearance toward the middle of the diaphysis. The total length of the right humerus is 10 mm, its proximal width is 1.5 mm, its distal width is 3 mm, and its minimum width is 1.5 mm.

As in other pachypleurosaurs, the radius (6.1 mm) is somewhat longer than the ulna (5 mm). The radius is fairly slender and evenly curved, with but slightly expanded proximal and distal heads. The ulna is shorter and broader than the radius and has a more distinctly expanded proximal head. A narrow spatium interosseum is defined by the two elements.

In the carpus, three ossified elements are pre-



FIG. 7. The right humerus of *Psilotrachelosaurus toeplitschi* Nopcsa, showing the ornamentation of the bone surface. Approximately 12 times natural size.

served, namely, the intermedium, ulnare, and distal carpal 4 (fig. 6A). The intermedium is a narrow but proximodistally elongated element, lying alongside the lateral side of the distal part of the radius, distal to the ulna (fig. 6B). The ulnare is a smaller, rounded element lying directly distal to the ulna. Distal carpal 4 is an even smaller ossification between the ulnare and the proximal head of metacarpal 4. Distal carpal 4 appears to be missing in the left carpus (fig. 6B), but this is most probably an artifact of rough preparation.

The metacarpals were judged to be of equal length by Sues and Carroll (1985), but the right manus shows a continuing yet slight increase in relative length from metacarpal 1 through 4 (metacarpal 5 is broken). This seems also to be true of the left hand, but there the metacarpals are less well exposed. The phalangeal formula cannot be established for either hand, but what is apparent on both sides is the relatively large size of the proximal phalanges as compared to the metacarpals. The best preserved digit is the third, and it shows that the metacarpal is about 10% longer than the proximal phalanx.

The right hindlimb (fig. 6C) is again better preserved than the left. The femur is a slender and only slightly curved bone, with the proximal head more strongly expanded than the distal end. It is slightly longer than the humerus. The total length of the right femur is 10.5 mm, its maximal proximal width is 2.8 mm, and its distal width is 1.6 mm. In the zeugopodium, the fibula (5.8 mm) is stronger and longer than the tibia (5 mm). The fibula is a strongly curved bone, with the distal head more distinctly expanded than the proximal head, and with a strongly concave medial border,

which results in a spatium interosseum (between fibula and tibia) that is wider than in the zeugopodium of the forelimb (between radius and ulna).

The well-preserved right tarsus (fig. 6C) shows three ossified proximal elements. The largest is the astragalus, which lies in an intermedium position, articulating both with the tibia (proximolaterally) and with the fibula (proximodistally); the smaller calcaneum lies directly distal to the fibula. Of the distal tarsals, only distal tarsal 4 is ossified; the bone is split horizontally (for which reason it does not show up in the photograph of the specimen; fig. 2), but it remains clearly identifiable, although it was neither figured nor described by Nopcsa (1928). Length measurements for the metatarsals and the corresponding phalanges are given in Table 1.

The phalangeal formula can be reconstructed for the right foot and must have been (in agreement with Nopcsa, 1928) 2-3-4-5-4. In the fourth digit, four phalanges are preserved, of which the fourth one is so small that it must represent the penul-

TABLE 1. Measurements of metatarsal (mt) and phalangeal length in the right pes of *Psilotrachelosaurus toeplitschi* Nopcsa.

	Metatarsal length (mm)	Length of corresponding proximal phalanx (mm)
mt1	approx. 2.9	?
mt2	3.5	1.5
mt3	4.3	2.7
mt4	4.7	3.2
mt5	3.8	2.2

timate one. Without the ungual (but including metatarsal 4), the length of the fourth digit is 12.3 mm. There is no evidence for hyperphalangy.

Discussion

The Pachypleurosauroidea (Pachypleurosauridae of Peyer, 1934) are known to include the genera *Anarosaurus*, *Dactylosaurus*, *Keichousaurus*, *Neusticosaurus*, *Psilotrachelosaurus*, and *Serpianosaurus* (see Introduction, above, and Rieppel, 1987, 1989a).

The genus *Keichousaurus* from the Middle Triassic of China (southwestern Keichow [Kiaochow] Province) is readily distinguished from all other pachypleurosaurs, including *Psilotrachelosaurus*, by a more distinctly curved humerus, a distinctly broadened ulna, and a transversally orientated intermedium positioned distal to the broad spatium interosseum between ulna and radius (Young, 1958, 1965). For these reasons, Kuhn-Schwyder (1959, p. 655) considered *Keichousaurus* a member of the family Nothosauridae, closely related to the genus *Lariosaurus*. However, skull characters as well as the structure of the sacral region clearly indicate the pachypleurosauroid status of *Keichousaurus* (Sues & Carroll, 1985; Lin Kebang, quoted in Sues, 1987).

Anarosaurus from the lower Muschelkalk of Remkersleben near Magdeburg (Germany) is readily distinguished from *Psilotrachelosaurus* by the lack of pachyostosis in the dorsal ribs and by its limb proportions. Originally described by Dames (1890), the holotype and only known specimen of *Anarosaurus pumilio* was reexamined by Nopcsa (1928) but destroyed during World War II (a second species, *Anarosaurus multidentatus*, is known only from an isolated lower jaw; Huene, 1958). The glenoid-acetabulum length of *Anarosaurus* is unknown due to incomplete preservation (following Nopcsa, 1928, *Anarosaurus* had a maximum of 21 dorsal vertebrae), but a cast of the original allows the measurement of the "standard length" (length of the centra of the last four presacral vertebrae, approx. 23 mm), length of left humerus (29.3 mm), and length of the right femur (36.5 mm). The humerus: standard length ratio is 1.26 for *Anarosaurus* and 0.83 for *Psilotrachelosaurus*. This indicates a smaller relative size of the humerus in *Psilotrachelosaurus*, which might be explained by the positive allometric growth of this bone (Rieppel, 1989a; Sander, 1989) and the larger

overall size of *Anarosaurus*. However, the humerus: femur ratio is 0.80 in *Anarosaurus* (0.97 in *Psilotrachelosaurus*), and the femur: standard length ratio is 1.57 in *Anarosaurus* (0.85 in *Psilotrachelosaurus*). These values indicate a disproportionally large femur in *Anarosaurus*, the proximal limb bone being distinctly longer than the humerus (at a larger overall body size) as compared to *Psilotrachelosaurus*. The relative size of the femur is diagnostic of the genus *Anarosaurus* (see also Sues & Carroll, 1985, p. 1608), and (again at larger overall size) the obturator foramen is not closed in *Anarosaurus* (as in the left pubis of *Psilotrachelosaurus*) but is represented by a distinct notch at the posterior edge of the pubis.

The genus *Dactylosaurus* from the lowermost Muschelkalk of Crony Slask (Upper Silesia) was first described by Gürich (1884, *Dactylosaurus gracilis*), but the type and only known specimen cannot be located today. Nopcsa (1928) described a second species, *Dactylosaurus schroederi*, which was recently restudied by Sues and Carroll (1985). It is presently not known whether the two species represent anything but ontogenetic variation within a single taxon. *Dactylosaurus* can be distinguished from *Psilotrachelosaurus* by a much more distinctly differentiated humerus (particularly in sex *y sensu* Rieppel, 1989a, and Sander, 1989), with a distinct deltopectoral crest, a prominent entepicondyle, and well-defined articular condyles (fig. 8). The bone lacks the surface ornamentation seen in *Psilotrachelosaurus* (Sander, 1989). The intermedium has rounded contours and lies distal to the spatium interosseum. Both manus and pes show a slight reduction of the phalangeal count (Sues & Carroll, 1985), which is not shared by *Psilotrachelosaurus* (the phalangeal count is known for the pes only).

The pachypleurosaurs from the Middle Triassic of Monte San Giorgio, Switzerland, are characterized by an apomorphic ornamentation of the surface of endochondral bone (Sander, 1989), which is also present in *Psilotrachelosaurus*. In addition to the latter genus, the clade comprises *Serpianosaurus* and *Neusticosaurus* (Carroll & Gaskill, 1985; Rieppel, 1989a; Sander, 1989). Within the clade, *Neusticosaurus* is derived with respect to the segmentation of the gastral ribs: these are composed of five segments in *Serpianosaurus* (the plesiomorph condition) but of only three segments in *Neusticosaurus* (Rieppel, 1987; Sander, 1989). Unfortunately, details of gastral rib morphology are unknown for *Psilotrachelosaurus*, but the genus differs from *Serpianosaurus* in the



FIG. 8. A series of humeri of *Dactylosaurus schroederi* Nopcsa (Institute of Geology and Paleontology of Tübingen Nr. GPTI 1744/1-10). Top row: sex y; bottom row: sex x (*sensu* Rieppel, 1989a; Sander, 1989).

strongly pachyostotic dorsal ribs, a lower count of dorsal vertebrae (19 in *Psilotrachelosaurus*, 20–23 in *Serpianosaurus*), the presence of ossified carpal/tarsal 4, and relatively shorter proximal limb bones (particularly a shorter femur; see table 2). *Psilotrachelosaurus* differs from *Neusticosaurus* in the broad pubis and ilium but shares with *Neusticosaurus* the pronounced pachyostosis of dorsal ribs as well as an elongated intermedium, oriented along the long axis of the limb and situated lateral to the distal head of the radius, distal to the ulna. Among pachypleurosaurs other than *Psilotrachelosaurus*, this morphology of the carpus is known only for *Neusticosaurus* (Zangerl, 1935; Kuhn-Schnyder, 1959), although variation in the shape of the intermedium is observed within the genus and its various species (Sander, 1989).

In the Middle Triassic of Monte San Giorgio, the genus *Neusticosaurus* is represented by three species (Carroll & Gaskill, 1985; Sander, 1989), which succeed each other in time. *Neusticosaurus pusillus* (Fraas, 1881; Seeley, 1882) comes from the Cava inferiore horizon of the lower Meridekalke, Ladinian, Monte San Giorgio, and equivalent deposits in northern Italy (also known from the Prosanto Formation, Ladinian, eastern Switzerland [Bürgin et al., 1991] and from the Dolomite of the Lettenkeuper, southwest Germany). *Neusticosaurus peyeri* Sander, 1989, comes from the

Cava superiore horizon of the lower Meridekalke, Ladinian, Monte San Giorgio, and equivalent deposits in northern Italy. *Neusticosaurus edwardsii* (Cornalia, 1854) is from the Alla Cascina horizon of the lower Meridekalke, Ladinian, Monte San Giorgio, and northern Italy. Comparison of *Psilotrachelosaurus* to the three known species of *Neusticosaurus* raises the question as to whether the only known specimen of the first genus represents a juvenile or an adult individual. Sander (1989) was able to study the postembryonic ontogeny of *N. pusillus* and *N. peyeri* in great detail, in particular as it relates to the differentiation of sexual dimorphism and the attainment of sexual maturity.

The carpal and tarsal bones do not ossify in *Neusticosaurus* until late in size class B (juveniles; Sander, 1989); in *Psilotrachelosaurus*, carpus and tarsus are well ossified, including a distal carpal/tarsal 4. The entepicondylar foramen is distally open in juvenile specimens of *Serpianosaurus* or *Neusticosaurus*. In *Psilotrachelosaurus*, the entepicondylar foramen is fully enclosed by bone and has retracted from the ossified distal margin of the humerus. This condition compares to a subadult (size class E of Sander, 1989) of *Neusticosaurus peyeri*, with a humerus length of about 9–10 mm. Presumed sexual maturity as indicated by the proportions and differentiation of the humerus is

TABLE 2. Number of dorsal vertebrae and limb proportions in *Psilotrachelosaurus toeplitzschii* Nopcsa compared to the genera *Serpianosaurus* and *Neusticosaurus*.

	<i>Psilotrache- losaurus</i>	<i>Serpiano- saurus</i>	<i>N. pusillus</i> (Monte San Giorgio)	<i>N. pusillus</i> (Lettenkeuper)	<i>N. peyeri</i>	<i>N. edwardsii</i>
Number of dorsal vertebrae	19	20–23	22–24	23–24	19–20	19–20
gle-ac: stand	4.66	3.91–4.80	3.79–5.46	4.21–5.44	3.45–4.48	3.66–4.58
hu: fe	0.97	0.75–1.23	0.88–1.15	0.87–1.03	0.90–1.30	1.24–1.84
hu: gle-ac	0.18	0.19–0.36	0.20–0.33	0.18–0.24	0.20–0.33	0.24–0.35
hu: stand	0.83	0.80–1.47	0.95–1.50	0.89–1.25	0.86–1.25	1.18–1.39
fe: gle-ac	0.18	0.21–0.32	0.22–0.30	0.20–0.29	0.21–0.25	0.16–0.21
fe: stand	0.86	0.97–1.20	0.97–1.40	0.91–1.50	0.79–1.06	0.65–0.96

Abbreviations: fe, femur length; gle-ac, glenoid–acetabulum length; hu, humerus length; stand, standard length.

reached in size class E (Sander, 1989). The smallest available individual of *Neusticosaurus peyeri* having reached apparent sexual maturity in sex y (as judged by the beginning differentiation of sexual dimorphism) has a standard length of 13.2 mm and a glenoid–acetabulum length of ca. 55 mm (Sander, 1989) and, hence, compares well with the size class of *Psilotrachelosaurus*; similar values obtain for *Neusticosaurus pusillus* (Sander, 1989). Sex x, however, remains closer to the juvenile condition in both proportions and morphology of the humerus (Rieppel, 1989a,b; Sander, 1989) and falls into size class E (subadults; Sander, 1989) as it reaches maturity. The conclusion therefore must be that, on the basis of humerus morphology and proportions, *Psilotrachelosaurus* represents a subadult (sex y) or a small but already sexually mature (sex x) individual.

Among the species of *Neusticosaurus*, *N. pusillus* (sample from Monte San Giorgio) differs from *Psilotrachelosaurus* by a higher vertebral count (22–24 dorsal vertebrae) and by relatively longer proximal limb bones (in both sexes; see table 2). The limb proportions of *Psilotrachelosaurus* more closely approach the proportions of a sample of *Neusticosaurus pusillus* from the German Lettenkeuper (Sander, 1989; table 2), but vertebral counts are again distinctly higher in the *Neusticosaurus* from Germany. As far as is known, distal carpal/tarsal 4 always fail to ossify in *Neusticosaurus pusillus* (Sander, 1989). Sander (1989) recognized a subpopulation of *Neusticosaurus pusillus* which shows a reduction in number of presacral vertebrae, reflected by a lower glenoid–acetabulum length: standard length ratio. However, although the values obtained for this subpopulation of *N. pusillus* (Sander, 1989, fig. 42) overlap with the value obtained in *Psilotrachelosaurus*, the relative limb proportions remain different (for the sub-

population of *N. pusillus*, the humerus: femur ratio is 1.0–1.25, the humerus: glenoid–acetabulum length is 0.26–0.32, and the femur: glenoid–acetabulum length is 0.24–0.28; for *Psilotrachelosaurus*, see table 2).

Neusticosaurus peyeri shares with *Psilotrachelosaurus* a lower count of dorsal vertebrae (19–20), and the proportions of the humerus and femur (as related to standard length) closely approach each other in the two species: the relative humerus length of *Psilotrachelosaurus* is at the lower end of the range of variation within *N. peyeri*, but the values for the relative length of the femur are closely comparable. However, *Neusticosaurus peyeri* shows a distinctly shortened trunk, as indicated by the glenoid–acetabulum length: standard length ratio (see table 2; the mean values for all specimens measured by Sander [1989] are *N. pusillus*, 4.62; *N. peyeri*, 3.89; *N. edwardsii*, 4.10; and *Psilotrachelosaurus*, 4.66).

Neusticosaurus edwardsii grows to larger overall size than can be extrapolated for *Psilotrachelosaurus*. Although the two taxa share a similar count of dorsal vertebrae (19–20) and a relatively short femur (see table 2), *Psilotrachelosaurus* differs from *N. edwardsii* (as also from *N. pusillus*) by a relatively short humerus. The smallest available specimen of *Neusticosaurus edwardsii* happens to be the holotype of this species (Carroll & Gaskill, 1985), with a glenoid–acetabulum length of 59 mm. Its proximal limb bones (humerus and femur) are relatively longer (as related both to standard length and to glenoid–acetabulum length) compared to *Psilotrachelosaurus* (for the type of *N. edwardsii*, the humerus: femur ratio is 1.13, the humerus: glenoid–acetabulum length is 0.28, the humerus: standard length is 1.3, the femur: glenoid–acetabulum length is 0.25, the femur: standard length is 1.15, and the glenoid–acetabulum: standard length

TABLE 3. Data matrix for the cladistic analysis of pachypleurosauroid interrelationships. Character definitions are given in the text.

	1	2	3	4	5	6	7	8	9	10	11
<i>Petrolacosaurus</i>	0	0	0	0	0	0	0	0	0	?	0
<i>Claudiosaurus</i>	0	0	0	0	0	0	0	0	0	0	0
<i>Youngina</i>	0	0	0	0	0	0	0	0	0	?	0
<i>Keichousaurus</i>	0	0	0	1	1	0	0	0	1	?	0
<i>Dactylosaurus</i>	1	0	0	0	0	0	0	1	0	0	0
<i>Anarosaurus</i>	1	0	?	1	?	?	?	1	0	0	0
<i>Psilotrachelosaurus</i>	?	?	0	1	1	0	?	1	1	?	1
<i>Serpianosaurus</i>	1	0 & 1	0 & 1	1	1	1	0	1	0	0	1
<i>N. pusillus</i>	1	0 & 1	1	1	1	1	0	1	1	1	1
<i>N. peyeri</i>	2	0 & 1	0	1	1	1	1	1	1	1	1
<i>N. edwardsii</i>	2	1	0	1	1	1	1	1	1	1	1

is 4.53; for *Psilotrachelosaurus*, see table 2). Again, distal carpal/tarsal 4 never ossify in *Neusticosaurus edwardsii* (Sander, 1989; contra Carroll & Gaskill, 1985). Sander (1989) also distinguished the bone ornamentation in *Neusticosaurus edwardsii* (his “orange peel” pattern) from that of other species (his “fingerprint pattern”). As indicated in the description of the humerus of *Psilotrachelosaurus*, the ornamentation of the endochondral bone surface may vary on different elements and in different locations of the same element. A systematic analysis of the variation of the ornamentation pattern throughout the skeleton of pachypleurosaur taxa is not yet available. On Sander’s (1989) criteria, the ornamentation pattern of *Psilotrachelosaurus* compares better to the one observed in *Neusticosaurus pusillus* and *N. peyeri* (as well as *Serpianosaurus*), than to that of *Neusticosaurus edwardsii*.

In 1959, Kuhn-Schnyder (1959) described a new pachypleurosaur, *Neusticosaurus “staubi,”* from the Prosanto Formation (Ladinian) of the eastern Alps of Switzerland. A comparison of the specimen to the abundant material from Monte San Giorgio (Sander, 1989; Bürgin et al., 1991, p. 970) revealed no taxonomically significant differences from *Neusticosaurus pusillus*. *Neusticosaurus “staubi”* must therefore be considered a species inquirenda and should at this time be referred to as *Neusticosaurus* sp. Peyer (1934) described poorly preserved specimens of “*Pachypleurosaurus*” (*Neusticosaurus*) from Perledo, northern Italy, but stratigraphical control on these early findings (dating back to the last century) is poor (A. Tintori, pers. comm.). Crude measurements taken from Peyer’s (1934) monograph for the best preserved specimen (“Bergamo” specimen) show relative limb proportions that fall into the range of vari-

ability of the Monte San Giorgio species and, hence, differ from *Psilotrachelosaurus* by the characters outlined above.

To assess the phylogenetic relationships of *Psilotrachelosaurus* within the Pachypleurosauroidea, a phylogenetic analysis was carried out based on D. L. Swofford’s software package PAUP (Phylogenetic Analysis Using Parsimony), version 3.0c (Swofford, 1989). *Youngina*, *Claudiosaurus*, and *Petrolacosaurus* were used as successive outgroups, based on an earlier analysis of sauropterygian interrelationships within diapsid reptiles (Rieppel, 1993). Character definition for the characters listed in the data matrix (table 3) is as follows.

1. Upper temporal fossa: Except for *Keichousaurus* (Young, 1958, 1965), pachypleurosaurs are characterized by a reduction of the size of the upper temporal fossa (1). The upper temporal fenestra is very small and slit-like or keyhole-shaped (2) in *Neusticosaurus peyeri* and *N. edwardsii* (Carroll & Gaskill, 1985; Sander, 1989), which may be correlated with the relatively great width of the skull table discussed by Carroll and Gaskill (1985) and Sander (1989).

2. In the plesiomorphic condition, the postorbital enters the margin of the upper temporal fossa (0) but is excluded therefrom in the apomorphic state (1).

3. The number of dorsal vertebrae is variable within taxa, and the range of variations overlap to some slight extent (*Serpianosaurus*, *Anarosaurus*). Twenty or fewer dorsal vertebrae are considered the plesiomorphic condition (1), 20 or more dorsal vertebrae the apomorphic condition.

4. A distinct and well-developed entepicondyle on the humerus is considered the plesiomorphic condition (0); its reduction is derived (1) within

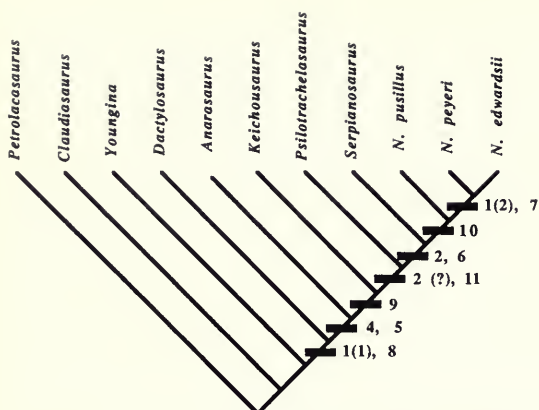


FIG. 9. Cladogram of pachypleurosauroid interrelationships. The characters are discussed in the text; their distribution among the taxa analyzed is coded in Table 3.

pachypleurosauroids. Other characters of the humerus are not used in this analysis because of sexual dimorphism (degree of development of the deltopectoral crest) or ontogenetic variation (closure of the entepicondylar foramen).

5. The pisiform may be present (0) or absent (1). Other characters of the forelimb were omitted from the analysis because of extensive variation, such as the shape and position of the intermedium. The distinctly broadened ulna is an autapomorphy of *Keichousaurus*, and hence uninformative in the analysis of interrelationships.

6. Distal carpal 4 may be ossified (0) or may fail to do so (1). The presence or absence of an ossified distal tarsal 4 is not coded separately, because the two characters generally show a congruent distribution.

7. The plesiomorphic number of phalanges in the manus is 2–3–4–5–3 (0); reduction of the phalangeal formula of the manus below 2–3–4–4–3 is coded as the derived condition (1). The formula 2–3–4–4–3 itself is still coded as plesiomorphic, because it may be accounted for by incomplete or problematical preservation (*Keichousaurus* [Young, 1958]; *Dactylosaurus* [Sues & Carroll, 1985]) or by ontogenetic variation (*Neusticosaurus* [Sander, 1989]). The reduction of the phalangeal count in the pes (beyond 2–3–4–4–3) is autapomorphic for *Neusticosaurus edwardsii* (Sander, 1989).

8. The plesiomorphic number of sacral ribs is two (0); three or more sacral ribs represent the derived condition (1).

9. Distinct pachyostosis of dorsal ribs is coded as the derived condition (1). The degree of pachy-

ostosis may vary ontogenetically, being weakly expressed in juveniles (Sander, 1989). However, distinct pachyostosis is absent in *Anarosaurus* and *Dactylosaurus*, two genera represented by specimens of adult age.

10. Gastral ribs composed of five segments represent the plesiomorphic condition; three segments per gastral rib is the derived character state (1).

11. The presence of surface ornamentation on the humerus is considered to represent the derived condition (1), as opposed to a smooth bone surface. This character is used here with the proviso that future studies may indicate ontogenetic variation or preservational bias in its distribution.

With the branch-and-bound search option implemented, and all characters treated as unweighted and unordered (character 1), the analysis yielded a single most parsimonious and fully resolved tree (fig. 9) with a tree length of 15 steps and a consistency index of 0.8 (rescaled consistency index 0.711). The Pachypleurosauroidea are diagnosed by a reduced upper temporal fossa (character 1), a feature carried to a greater extreme in the sister-taxa *Neusticosaurus peyeri* and *N. edwardsii*; the relatively large upper temporal fossa of *Keichousaurus* is best interpreted as a reversal (based on ACCTRAN and DELTRAN character optimization strategies). The presence of three sacral ribs (character 8) is a second synapomorphy of the Pachypleurosauroidea, again reversed in *Keichousaurus* (see below).

Within the Pachypleurosauroidea, *Dactylosaurus* is shown as sister-taxon of all other genera, which share the derived absence of a well-developed entepicondyle on the humerus (character 4) and of a pisiform in the carpus (character 5; this character is not known in *Anarosaurus*). *Keichousaurus* groups with *Psilotrachelosaurus*, *Serpianosaurus*, and *Neusticosaurus* on the basis of rib pachyostosis (character 9), which implies that the presence of two sacral ribs (Lin Kebang, cited in Sues, 1987) is to be treated as a reversal in this genus, whereas absence of rib pachyostosis in *Serpianosaurus* is also a reversal.

Psilotrachelosaurus finally is shown to be the sister-taxon of the *Serpianosaurus*–*Neusticosaurus* clade, a relationship supported by the shared presence of surface ornamentation on the humerus (character 11). The *Serpianosaurus*–*Neusticosaurus* clade shares the (variable) exclusion of the postorbital from the upper temporal fossa (character 2), a character that is unknown in *Psilotrachelosaurus*. Another derived character shared by

the *Serpianosaurus*–*Neusticosaurus* clade is the lack of an ossified distal carpal/tarsal 4 (character 6). *Neusticosaurus* finally is diagnosed by gastral ribs composed of three segments (character 8), and, within this genus, the species *peyeri* and *edwardsii* form sister-taxa on the basis of a reduced phalangeal count in the manus (character 7). *Neusticosaurus pusillus* is diagnosed by a high number of dorsal vertebrae (overlapping to some degree with *Serpianosaurus*).

Conclusions

Psilotrachelosaurus is redescribed and recognized as a distinct taxon, closely related to the *Serpianosaurus*–*Neusticosaurus* clade of the Middle Triassic from the southern Alps and the German Muschelkalk. It shares with this clade the derived surface ornamentation on endoskeletal elements but differs from it in the retention of an ossified distal carpal/tarsal 4, the relatively broad ventral elements in the pelvic girdle (pubis and ischium), and body proportions, in particular a proportionately short humerus (as related to standard length).

Serpianosaurus is so far known only from the Grenzbitumenzone (Anisian–Ladinian boundary), followed by species of the genus *Neusticosaurus* in stratigraphical succession (Sander, 1989). As discussed above, a late Anisian or early Ladinian age can be ruled out for *Psilotrachelosaurus*. However, as *Psilotrachelosaurus* is the sister-group of the *Serpianosaurus*–*Neusticosaurus* clade, the conclusion must be that *Psilotrachelosaurus* and *Serpianosaurus* share the same minimal geological age, i.e., that the clade of pachypleurosauroids represented by *Psilotrachelosaurus* must date back to the Anisian–Ladinian boundary (Rieppel, 1986; Norell & Novacek, 1992).

Zapfe and König (1980, p. 70) describe the transition between the late Anisian Zwischendolomit and the basal layers of the lower unit of the Partnach-Plattenkalk in the Kellerberg profile as being very similar to the Grenzbitumenzone of Monte San Giorgio (which comprises the Anisian–Ladinian boundary) in terms of both lithology and facies (Bechstädt & Mostler, 1974, p. 50). *Psilotrachelosaurus* as well as *Lariosaurus* come from geologically younger deposits (middle Ladinian) of the Gailtaler Alps, stratigraphically equivalent to deposits at Monte San Giorgio (lower Meridekalke) that have yielded hundreds of specimens of *Neus-*

ticosaurus but, for some unknown reason, not a single *lariosaur*. Depositional conditions again seem to have been rather similar at both localities (Rieber, 1968, 1973; Zorn, 1971; Warch, 1979, 1984). And whereas a coexistence of *Lariosaurus* and pachypleurosaurs may have occurred during the deposition of the Grenzbitumenzone (*Lariosaurus buzzi* Tschanz, 1979, represented by a single specimen of controversial generic identity; see Kuhn-Schnyder, 1990; Rieppel, in press), *Lariosaurus* is otherwise known at Monte San Giorgio only from the upper Meridekalke (upper Ladinian [Kuhn-Schnyder, 1987]; *Lariosaurus lavizzarii* is a junior synonym of *L. balsami* [see Tschanz, 1989]), deposits, which have not yielded any pachypleurosaur material. Other than in the Gailtaler Alps, a coexistence of *Lariosaurus* and pachypleurosaurs is known from the Calcare di Perledo, most probably of late Ladinian age (see discussion under Geological Provenance). Further analysis of the temporal as well as geographical distribution of *lariosaurs* and pachypleurosaurs might provide important insights into the synecological relationships between these morphologically quite similar, but only distantly related taxa.

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